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DOES FUNCTIONAL REDUNDANCY STABILIZE FISH COMMUNITIES?

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ABSTRACT

Functional redundancy is a community property thought to be contributing to ecosystem resilience. It is argued that trophic (or other) functional groups with more species have more linkages and opportunities to buffer variation in abundance of individual species. We explored this concept with a 30-year time series of data on 83 species sampled in the IBTS trawl survey.

Our results were consistent with the hypothesis that functional redundancy leads to more stable (and by inference more resilient) communities. Over the time series trophic groups (assigned by diet, size (Lmax) group, or both factors) with more species had lower CVs in abundance and biomass than did trophic groups with fewer species. These findings are also consistent with Bernoulli's Law of Large Numbers, a rule that does not require complex ecological and evolutionary processes to produce the observed patterns. Through iterative randomizations of the species' time series into groupings of the same sizes as the functional groups, we developed expected pdfs of CVs in abundances and biomasses, assuming only the Law of Large Numbers was at work. The observed CVs of all groupings were not significantly different from these simulated distributions.

These results do not prove the absence of ecological processes contributing the greater stability of functional groups with more redundancy, however they do not justify invoking any such processes. The results support management approaches that maintain species richness, but do not require management to try to protect complex (and poorly understood) ecological processes.

Key words: Functional redundancy, Resilience, Stability, Neutral model, Ecological process

APOLOGIA

The material presented in this talk is currently under revision for potential publication in the ICES Journal of Marine Science. To avoid compromising the journal through pre-publication of the same material in this CM document, here we will only present the main points of the complete paper, key results, and point-form highlighting of the implications of the results. Look for the full presentation of material, with the same title and authors, coming soon to a journal website near you!

QUESTION BEING INVESTIGATED

One argument for why conservation of biodiversity is important for protecting ecosystem structure and function is that "redundancy" in ecosystem functions contributes to system "resilience" (Tilman 1996, Rosenfeld 2002, Brooks et al. 2005, Worm et al. 2006). It is argued that having several species within the same trophic functional group helps ecosystems maintain their characteristic structure and functions. Functional redundancy, also referred to as the “portfolio effect” (Schindler et al. 2010), provides multiple pathways that make ecological processes more resistant to perturbations of the abundance of individual species, since other pathways can compensate for any change in the function served by the species whose abundance initially was perturbed (Hui 2006, Shackell and Frank 2007, Reecht et al. 2009). This hypothesised linkage between functional redundancy and ecosystem resilience is leading to the maintenance of functional diversity itself being promoted as a management objective to maintain ecosystem processes in an uncertain world.

Our concern was whether the resilience was a result of active compensation mechanisms within the functional groups, such that ecological mechanisms caused reciprocal, *compensatory* variations among the species in the same functional group, sharing a common carrying capacity. This is important because there is an alternative explanation for greater stability in aggregate population status being observed in larger functional groups. As far back as Bernoulli (1713), the Law of Large Numbers has been well established: the average (or sum) of independent, randomly varying numbers becomes proportionately less variable as more numbers are averaged (or summed). This would make the “compensation mechanisms” simply statistical rules, not requiring protection of specific ecological processes (Schindler et al. 2010).

In our study we indirectly evaluate the strength of active compensation processes at the scale of function groups using a neutral model approach. Using the North Sea International Bottom Trawl Survey (IBTS) time series, we first ask if larger functional groups in the survey data are indeed more stable than smaller functional groups. If they are, then we next account for the statistical effect expected from merely the Law of Large Numbers. If that statistical process, by itself, is insufficient to account for the greater stability of larger functional groups, then there is indirect evidence that active compensatory mechanisms are present within functional groups. However if the law of large numbers is sufficient to account for the greater stability of larger functional groups, then there is little basis to invoke active compensatory processes to account for the increase in stability.

METHODS

We used the North Sea IBTS trawl survey, with the standardizations and screening for invalid records described in Daan (2005) to provide a consistent time series of survey abundance and biomass estimates from 1977 to 2009 for the 83 most common fish species (including elasmobranches) above 5 cm. Abundance (numbers by species by year) were converted to biomass by transforming the survey length frequencies by species and year using the general equation $W = 0.01L^3$. We standardized individual species abundances and biomass estimates to a common unit mean and variance, for two reasons. First, species differ greatly in absolute abundance and catchability by the survey gear, so analyses using raw observations were dominated by variation in abundance of a few of the most common and catchable species. Second, adjustments to exactly match the "compensation ability" of a single individual or kilogram of any one species relative to single individuals or kilograms of other species in a functional group, would have to take account of all the relevant sampling (catchability) and ecological (behaviour, physiology, distribution, etc) factors that could affect compensation ability. Such species by species (and possibly pair by pair) adjustments to observations are far beyond current ecological knowledge. The standardization we used ensures the range of variation of all species is equal, so any one individual (abundance) or kg (biomass) can "compensate" fully for any other within a functional group. We assume this is an upper cap on true compensation ability within functional groups, whether compensation is expressed by individual or by weight. If compensation is incomplete or diffuse, our standardizations are likely to inflate the likelihood of finding evidence of compensatory variation in either data set, a bias we take into account in our analyses and discussion.

Functional Groupings: Each of the 83 species was categorized into one of six initial trophic groups based on diet data (Daan 1989, Hislop 1997, Greenstreet et al. 1997, Jennings et al. 2002, Heath 2005, Stelzenmuller et al 2009) and one of size L_{max} groups based on length data (Daan et al. 2005, Pope et al. 2006, Gislason et al. 2010). Species used and their diet and L_{max} classifications are listed in Annex 1.

Testing for the "portfolio effect": The different functional groups identified have different numbers of species, such that the aggregate abundance or biomass of a group with many species was larger than the aggregate abundance or biomass of small groups. Consequently the hypothesis that larger numbers of species in a functional group results in greater aggregate stability over time was tested with CVs of abundance or biomass over years. If the null hypothesis of equal CVs regardless of size of functional groups is rejected then the aggregate abundance or biomass of larger functional groups should be relatively more stable than the aggregate abundance or biomass of small functional groups.

Testing for the presence of ecological processes: We used neutral modelling to test if any of the variances differ from the expected variance if only the Law of Large Numbers was acting. To get the expected variances we randomly sorted without replacement the species into groups of the same size (numbers of species) as observed for the functional groups in the North Sea. We then calculated the annual mean abundance or biomass in each randomly assigned "functional group" and the variance of mean abundance or biomass in each functional group over the full time series. The observed variance of the aggregate abundance or biomass of each functional group was compared to a frequency distribution of 500 expected variances based on only the Law of Large Numbers and the individual patterns of

variation in each species' abundance or biomass over time. Results are presented separately for each dietary group, each Lmax group, and for dietary-Lmax groupings, for all groupings with four or more species in the actual North Sea fish community. Within each of the three classifications, probabilities were combined across the categories using Fisher's method for combining independent probabilities, to give an overall evaluation of the likelihood that the set of probabilities would have been observed under the Null Hypothesis of only the Law of Large Numbers being at work.

RESULTS

For all three classification criteria the CV of is inversely correlated with the number of species in a group for both abundance and biomass. Despite small samples sizes of numbers of groups per classification criterion, negative correlations were highly significant for Lmax (abundance) and for the groups tested in aggregate for biomass, whether the 17 groups were considered independent (biomass $r = -.57$, $P<0.01$ and abundance $r = -0.59$, $P < 0.01$), or a more conservative test of using Fisher's method to combine the probability of the correlations of the three groups (biomass $P=0.048$ and abundance $P=0.027$). The Null Hypothesis of independence between group size and relative variation in abundance over time is rejected for both biomass and abundance. Large functional groups have greater relative stability in abundance.

For the second Hypothesis, testing whether sample size alone was adequate to account for this effect, the variance of the "real" groupings was well within the distribution of simulated variances, whether examined by diet group, by Lmax group, or by the combined diet-Lmax group. Observed (arrow) and expected frequency distributions assuming only the Law of Large Numbers is responsible for the negative correlation of CV with functional group size are presented for the individual groups are displayed in Figures 1 and 2. Statistically, when the tests of combined probabilities are considered, the results from all three grouping criteria are likely to be observed by chance for abundance:

Lmax Groups $\chi^2 = 9.66$ df = 12, P=0.64, Diet Groups $\chi^2 = 6.43$, df = 8, P = 0.60, P = .66, Diet-Lmax Groups $\chi^2 = 16.49$, df = 14, P = 0.28).

And for biomass:

Lmax Groups ($\chi^2 = 9.53$, df =12. P = 0.66, Diet Groups $\chi^2 = 5.83$ df = 8, P = .67, Diet-Lmax Groups $\chi^2 = 13.60$, df = 14, P = 0.48.

IMPLICATIONS

We find that functional redundancy does lead to greater stability of abundance and biomass over time for the North Sea fish community. However, the Law of Large Numbers is sufficient to account for the observed reduction in relative variation over time. We found no evidence to support invoking additional ecological processes as necessary to provide more stable abundances or biomasses of suites of North Sea fish species, whether they are functionally similar in diet, of the same Lmax class, or a combination of the two.

This does not mean that functional redundancy does not contribute to community resilience. Our analyses are consistent with the arguments that functional redundancy *does* contribute to community resilience, and therefore its conservation is a legitimate candidate as a management objective. We suggest that management should still strive to protect the diversity of species in functional and size groups to get the potential benefits of the portfolio effect, and loss of any species in a functional group should be prevented, to maintain the robustness of the full system. However, robust management strategies could be formed to achieve such objectives without waiting for detailed ecological studies of the interactions among the species within the various diet or Lmax groups.

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Figure 1. Frequency distributions of simulated variances of abundance data for Lmax groups (Column 1, A-F), diet groups (Column 2, G - J), and combined diet – Lmax groups (Column 3, K-Q). The observed variances for the real data are represented by an arrow within each figure. Categories of A-F = <10, 10-20, 20-40, 40-80, 80-160, and >160 (all cm). Categories of G-H = demersal benthivore, demersal piscivore, Ppis: pelagic piscivore, pelagic planktivore. Categories of K-Q = Dben. 10-20, Dben. 20-40, Dben. 40-80, Dben.80-160, Dpisc. 40-80, Dpisc. 80-160, Dpisc. 160+ (abbrevisions : Dben: demersal benthivore, Dpis: demersal piscivore, Ppis: pelagic piscivore, Ppla: pelagic planktivore).

Figure 2. Frequency distributions of simulated variances of biomass data for Lmax groups (Column 1, A-F), diet groups (Column 2, G - J), and combined diet – Lmax groups (Column 3, K-Q). The observed variances for the real data are represented by an arrow within each figure. Categories of A-F = <10, 10-20, 20-40, 40-80, 80-160, and >160 (all cm). Categories of G-H = demersal benthivore, demersal piscivore, Ppis: pelagic piscivore, pelagic planktivore. Categories of K-Q = Dben. 10-20, Dben. 20-40, Dben. 40-80, Dben.80-160, Dpisc. 40-80, Dpisc. 80-160, Dpisc. 160+ (abbrevisions as in Figure 1).

FIGURE 1

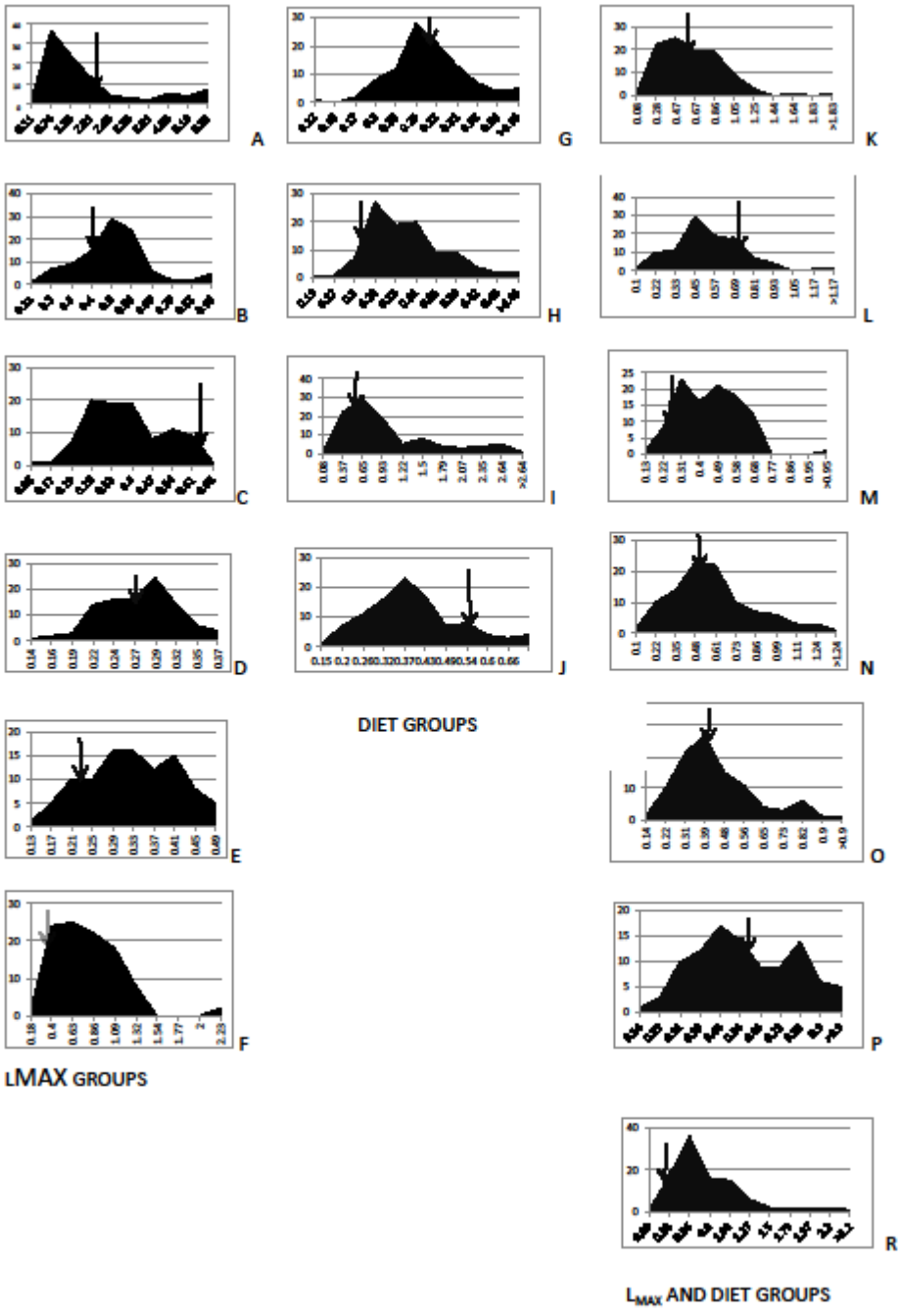
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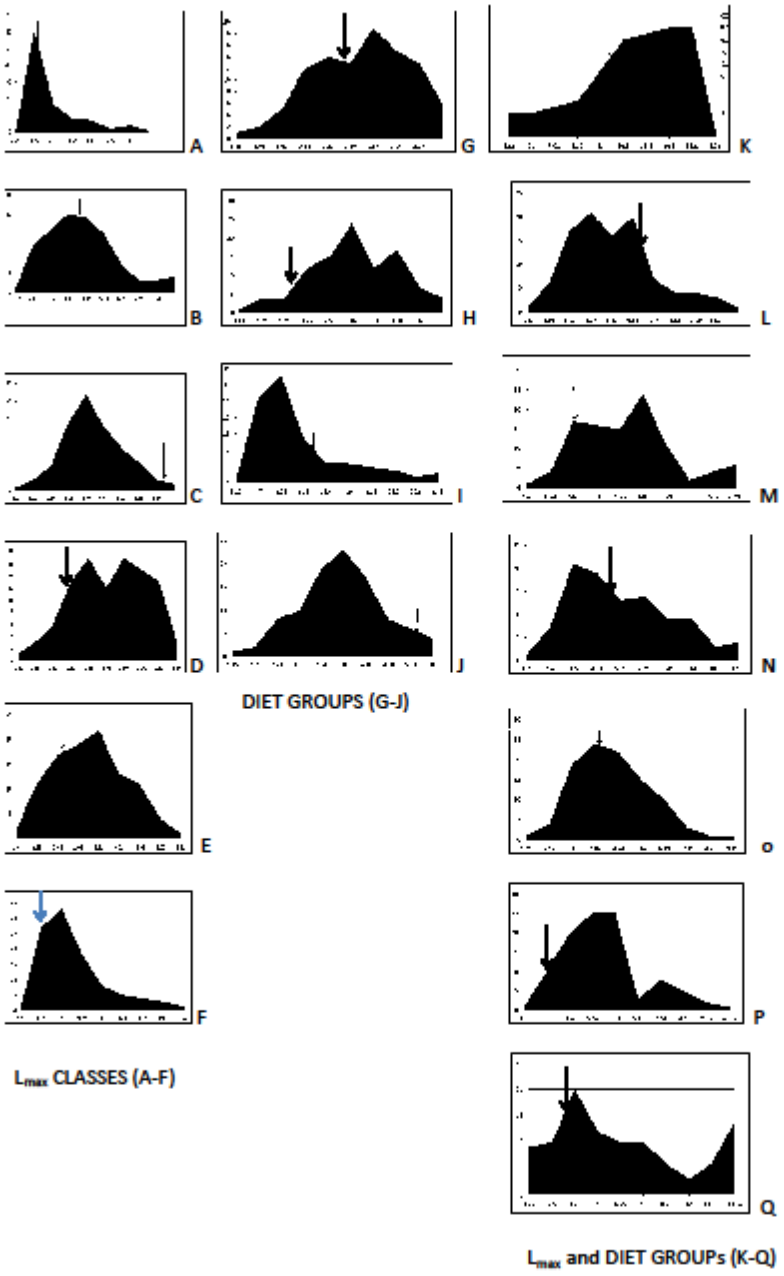
Figure 2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